CHAPTER 3

Chance in the Modern Synthesis

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The modern synthesis in evolutionary biology is taken to be that period in which a consensus developed among biologists about the major causes of evolution, a consensus that informed research in evolutionary biology for at least a half century. As such, it is a particularly fruitful period to consider when reflecting on the meaning and role of chance in evolutionary explanation. Biologists of this period make reference to "chance" and loose cognates of "chance," such as: "random," "contingent," "accidental," "haphazard," or "stochastic." Of course, what an author might mean by "chance" in any specific context varies.

In the following, we first offer a historiographical note on the synthesis. Second, we introduce five ways in which synthesis authors spoke about chance. We do not take these to be an exhaustive taxonomy of all possible ways in which chance meaningfully figures in explanations in evolutionary biology. These are simply five common uses of the term by biologists at this period. They will serve to organize our summary of the collected references to chance and the analysis and discussion of the following questions:

- What did synthesis authors understand by chance?
- How did these authors see chance operating in evolution?
- Did their appeals to chance increase or decrease over time during the synthesis? That is, was there a "hardening" of the synthesis, as Gould claimed (1983)?

HISTORIOGRAPHICAL NOTE

What was the synthesis? When did it begin, and when did it end? Who were the major participants? And what did they synthesize? There is a good deal of debate among historians of biology about the meaning of the synthesis: its aims and scope, its participants, and when it began and ended (see, e.g., Burian 1988; Gayon 1998; Cain 1994; Smocovitis 1994b, 1994a, 1996; Depew and Weber 1995; Largent 2009; Cain and Ruse 2009; M. J. S. Hodge 2011; Delisle 2009, 2011; Provine 1971). We grant that there is no single way to tell the story of the synthesis; so we choose to be ecumenical and include as many potentially relevant figures as possible and as permissive a periodization as possible (though we must be selective in our discussion of representative figures, due to limitations of space). Arguably, the earliest influential document of the twentieth century that qualifies as synthetic is R. A. Fisher's "The Correlation between Relatives on the Supposition of Mendelian Inheritance" (1918), which established the compatibility of a multifactorial (or Mendelian) theory of inheritance with a "biometrical" view of quantitative traits, or traits with continuous distribution, which selection might gradually shift over time. This laid the groundwork for what is sometimes called the orthodox view of the synthesis, as explained and defended in Mayr and Provine's (1980) volume, according to which the major figures of the synthesis came to broad agreement on the view that gradual selection on minor genetic variants is largely responsible for the diversification and adaptation we see today. Macroevolution—the divergence of species and lineages—does not require appeal to causal factors over and above those deployed in microevolutionary theory, according to this orthodox view. The major texts of the synthesis provided arguments and evidence in support of this general theoretical agreement.

The "orthodox" view, of course, foregrounds agreement upon empirical and theoretical principles of evolution, but it is also surely the case that the synthesis was constituted by self-conscious actors, who aimed at the formation and institutionalization of the discipline of evolutionary biology. In the 1940s, Mayr launched the Society for the Study of Evolution and its associated journal, *Evolution*; he also was instrumental in organizing important meetings, drawing together biologists with different areas of specialization from around the globe to establish a more interdisciplinary biology, and establishing centers of research and common curricula. That is, the synthesis was not only a scientific change, but also a sociological and institutional one (Cain 1994; Smocovitis 1994b, 1994a). The name "modern synthesis" was coined by Julian Huxley (1942), whose book *Evolution: The Modern Synthesis*

was both a comprehensive overview of then current biology and an articulation of a research program. The theoretical work and organizational events of the synthesis spanned roughly three decades, from about 1920 to 1950.

This period exhibited a fluctuation of views about the role(s) of chance in evolution, eventuating in a "hardening," or emphasis on selection (Gould 1983) that continued well past the synthesis period. The stabilization of the modern synthesis view on chance (insomuch as there was a stable view) was established firmly in the 1940s, and the major texts of this period all significantly drew upon the population genetic documents published during the "early phase" of the modern synthesis, primarily accomplished by Haldane, Fisher, and Wright in the 1920s and 1930s. Significant further work was done in the 1940s and '50s, making clear the relationships of ecology to evolution and of paleontology to systematics.

In contrast to the "orthodox" view just described, Cain (2009) proposes that we abandon the "unit concept" of the evolutionary synthesis altogether and suggests that we shift focus to a wider range of transformations in the biological sciences during the 1930s. Historians' prior assumptions that the synthesis was a single event, bounded in time, that there was a single theory endorsed by synthesis participants, and the very idea that "conjunction is meaningful," he claims, are all mistaken. Instead, Cain argues that we should focus on "organizing threads" of research into the nature of species and speciation, experimental taxonomy, and the shift from object- to process-based biology. We agree that historians ought to be wary of identifying the synthesis exclusively with agreement on what we have called the orthodox view above. Cain usefully suggests that we should think of the period as one involving "problem complexes." He identifies four: selection, variation, heredity, and divergence. To be sure, all four problems were central matters of interest for biologists during this period. But there are different and perhaps equally informative ways to decompose the synthesis. For instance, Gayon's comprehensive *Darwinism's Struggle for Survival* (1998) focuses on different yet nonetheless core problem complexes: defending "Darwinism" from its (perceived) detractors and integrating genetics with evolution. To be clear, we don't see these approaches as in opposition, but simply as focusing on distinct aspects of the same historical period, akin to Wimsatt's view that the same system can be decomposed in multiple ways (Wimsatt 1972). Not unlike the fruit fly, the modern synthesis is a complex historical process that can be decomposed in many different ways.

We contend that a variety of problem complexes, goals, questions, and methods—theoretical as well as pragmatic or institutional—is not incompat-

ible with general agreement on certain core views about evolutionary change. While the retrospective emphasis on classical population genetics may have been oversold (as historians of population genetics themselves have argued; see, e.g., the new preface to Provine 1986 in the 1989 edition), there was certainly agreement upon a core set of commitments, what Burian has called a "meta" theory (Burian 1988) or *research program*, in service of addressing a suite of questions about the evolution and diversity of life. What was important to authors of the late synthesis was not what the models of classical population genetics required, but what they permitted. The core elements of the classical models describe how evolution would progress, under certain assumptions, leaving open to empirical investigation how frequently those assumptions are met in the world. Thus, different synthesis authors were free to disagree on the relative significance of selection and drift. Nonetheless, we contend that there was a shared family of commitments about *the operation of chance in evolution throughout the synthesis*, at the level of segregation and assortment of genes, patterns of mating, probabilistic processes like selection, and "random" events (such as floods or earthquakes) that might lead to ecological or geographical isolation. We turn now to a characterization of these distinct forms of chance.

FIVE SENSES OF CHANCE

There were (at least) five different senses of chance at play in the synthesis.[1] First, one might assume appeals to chance in science to be making metaphysical claims about the world as *fundamentally indeterministic*. Only rarely, however, is the question of determinism or indeterminism addressed overtly during the synthesis. Dobzhansky (1956, 1962, 1967) and Haldane (1942) wrote works toward the end of their careers that touched on philosophical issues such as free will and indeterminism, and interest in such questions was a lifelong passion of Sewall Wright (Provine 1986). However, through 1950, when appealing to chance, most synthesis authors were silent about "quantum indeterminacy." Indeterminism in physics did play an important role for Fisher (1934), and we will discuss this in further detail below. But for the most part, when discussing chance, such authors are referring to events and processes at a relatively macro scale: segregation of genes, isolation of small subpopulations, and so on.

Second, the term *chance* is sometimes used interchangeably with *random*. There are more and less precise senses of *random*; the most precise sense is the notion of a *random variable*. Random sampling from a uniform distribu-

tion results in outcomes that are equiprobable; sampling from nonuniform distributions results in outcomes that are not equiprobable. When speaking of random mating or random sampling of alleles in the process of meiosis, most synthesis authors appear to be referring to a sampling process whose outcomes are assumed to be equiprobable. Or, in such cases, the outcome (of a mating with type X or Y, or allocation of allele *A* or *a*) is spoken of as random, simply in the sense that two (or more) outcomes are equiprobable. Other times when authors referred to random mutation, they meant "random with respect to fitness" (i.e., mutation was not "directed" or a response to environmental challenges, as some Lamarckians claimed). Sometimes, however, when an event like mutation was spoken of as random, the author may have meant that its chance of occurring is unpredictable (in the epistemic sense) or, in contrast, is due to indeterministic processes (ontic). The ambiguity may have been deliberate, as so little was known about the mechanisms underpinning mutation at this point (Sahotra Sarkar, pers. comm., April 13, 2013). That is, given the limited understanding of the structure of the gene and the causes of mutation at the molecular and submolecular levels at the time, the authors indeed meant that they were unsure about the relevance of quantum indeterminacy (though see, e.g., Sloan and Fogel 2011 for a discussion of the "Three-Man Paper" and the role of radiation in mutation at the time).

Third, and most often, *chance* is frequently used as a *proxy for probability*. For instance, possession of a trait might raise (or lower) the chances of some outcome. All synthesis authors speak of natural selection as a matter of probabilities, or as probabilistic in this sense: even exceptionally high fitness does not guarantee survival or reproductive success, but only increases in organisms' "chances." Likewise, the chance (probability) that a random gene combination is adaptive was thought to be very low (S. Wright 1932, 358). The chances of various outcomes are thus spoken of as "high" or "low," when outcomes are *unequally probable*.

Fourth, events such as floods, storms, meteorites crashing into the earth, and volcanoes are sometimes spoken of by synthesis authors as chance, random, or, interchangeably, contingent events. Such events are chancy in the sense that they are rare and they *result in (usually nonfortuitous) outcomes for organisms, lineages, and species, which are unusual, "unlucky" or not predictable*, given existing biogeography, survivorship, or ongoing ecological circumstances. Volcanic explosions, mutations, lightning strikes, and other random events in this sense are uncorrelated (either as events or in their effects)

with other causes that shape evolution (e.g., selection). In other words, such events *disrupt current trends*—by dividing landscapes, wiping out resources, or eliminating or isolating groups that would otherwise be physically continuous and interbreeding.

Fifth, and finally, *chance* is often used to refer to *outcomes in contradistinction to, or "opposing" selection*. Wright speaks of both drift and mutation as "chance" factors that "oppose" selection (S. Wright 1932, 359). Admittedly, this is in part due to the fact that the outcomes of drift and mutation are random, in the second sense defined above. For a particular trait and environment, selection will have a predictable "direction," whereas drift and mutation result in outcomes that are (relatively) unpredictable. Such chance outcomes are not "directed," either toward some desired (adaptive) outcome or toward any outcome in particular. Most synthesis authors assumed that mutations were most often deleterious. So the direction of mutation *was* predictable in the sense that it was generally assumed that adaptive mutations are rare. Second, the direction of drift at the population level is a reduction in heterozygosity, as small sample sizes of finite populations are likely to have a smaller representation of variation than the original population sampled. In this sense, at least, drift results in a "predictable" outcome. Nonetheless, many synthesis authors often assimilated "non-directional" changes in gene frequency with whatever "opposes" the direction of selection. This, though, should not be interpreted as the claim that drift is "whatever we cannot explain"; synthesis authors were at pains to identify which empirical facts are of relevance to testing claims that one of the two factors was at work, and how.

In sum, what synthesis authors meant by chance in any particular instance was context dependent. A chance event was often defined in terms of a contrast, for example, with a "directional" cause, process, or tendency, or a predicted outcome. Appeals to chance events or outcomes were often in *contradistinction to, or "opposing," a particular predicted outcome*. Given the rarity of adaptive mutations, one often cannot predict, for example, when and where a fortuitous mutation will come about; nor can one predict whether isolation of a small subpopulation will yield a fortuitous gene combination. Such events might then be spoken of as "due to chance," which is just to say that the author did not know precisely when particular such events would occur, though he or she could predict that, as a general category, such events are rare. And an author could model chance processes as akin to processes of random sampling, one of the insights that theoretical population geneticists brought to the table.

AIMS AND METHODS

Our aim here is to survey the uses and meanings of these terms in the context of the early and later synthesis, as well set their use(s) in a larger context in order to address the questions we laid out in the introduction.

We document below uses of the term *chance* and its (loose) cognates *random*, *probable*, *by accident*, and so forth in the major texts of the synthesis authors. We realize that the choice of major texts is somewhat arbitrary. However, in part due to limitations of space, we opted to focus on those texts that we see as representative of key views on the role of chance by major figures in the synthesis period: Fisher's *The Genetical Theory of Natural Selection* (1930), Wright's 1931 and 1932 papers; Dobzhansky's first (1937) and third (1951) editions of *Genetics and the Origin of Species*; Mayr's *Systematics and the Origin of Species* (1942); Simpson's *Tempo and Mode in Evolution* (1944); and Stebbins's *Variation and Evolution in Plants* (1950).[2] We have chosen to compare early and late editions of Dobzhansky's *Genetics and the Origin of Species* because they illustrate in a striking way a shift of perspective on the relative significance of chance in evolution over the course of what Gould (1983) has called a "hardening" of the synthesis.

Understanding how and in what sense chance was understood by synthesis authors requires more than a summary of their particular views; also required are a careful comparison and contrast of their distinct uses of the term and its cognates and an understanding of its relevance to the process of evolution. The synthesis authors referred to chance not infrequently, but, as we've said, with meanings that depended importantly on context. By and large, the most common use of the term *chance* is simply as proxy for *probability* or *probable*, as in, "the chances of fixation of a novel gene are low in a small population." The second most common is as a proxy for *random*. "Chance," or "random," mating occurs when distinct types of organism in a population may be equally likely to mate with one another.

Many authors treat senses four and five above interchangeably. That is, authors are often unclear in any case whether "chance" might refer to unusual events that disrupt current trends—such as floods, earthquakes, and so forth, or "forces" that act "contrary" to selection. For instance, Stebbins argued that certain correlations between various morphological characteristics are so strong as to rule out "their origin by chance," which is to say that they are unlikely to be due to chance fixation of alleles and more likely to be due to selection. In other words, when a correlation between environment and trait

is strong, synthesis authors were more likely than not to expect an explanation that might appeal to natural selection.

Finally, one general trend we noticed in the literature surveyed below is that the frequency of appeals to chance in the sense of drift as an explanatory factor in evolution appears to shift back and forth from the early to the later synthesis. While early synthesis authors like Fisher and Haldane thought drift to be a relatively unimportant factor in adaptive evolution, Wright's emphasis on drift influenced Dobzhansky's first edition of *Genetics and the Origin of Species* (1937), which exhibits an emphasis on chance factors, particularly in speciation. Dobzhansky's appeal to chance factors (e.g., isolation and drift), in explanations of speciation and nonadaptive differences between species, was far more common in the 1937 edition of *Genetics and the Origin of Species* than in the 1951 edition. A shift in emphasis toward selection over drift as a major factor in evolution in later editions supports Gould's (1983) thesis that there was a "hardening" of the synthesis, or progressively greater emphasis on adaptation and selection. With this overview in mind, we now offer a historical perspective on how each synthesis author viewed chance in evolution.

THE EARLY SYNTHESIS

This period—roughly 1918–35—is when Haldane, Fisher, and Wright developed a general mathematical representation of Darwinian evolution in populations, on a Mendelian theory of inheritance. Evolution was represented as changes in the relative frequency of genes, due to selection, mutation, migration, and drift, or random sampling of alleles, from one generation to the next. All saw themselves as resisting views that they understood as in tension with orthodox Darwinism: Lamarckian, "orthogenetic," and other "directed" views of evolution. Such theories invoked factors outside of mere selection, mutation, migration, and drift as shaping the direction or character of change in populations over time. All argued that selection on slightly varying characters was sufficient (over evolutionary time) to generate the diversity and adaptive variation we find currently. However, Wright believed that isolation of subpopulations and "random fluctuation of gene frequencies" enabled populations to move to novel "adaptive peaks," escaping suboptimal gene combinations (S. Wright 1931, 1932).

Fisher

Fisher was a "synthesis" thinker in the broadest possible sense; his aim was not only to synthesize Darwinism and Mendelism, but also to discover the fundamental "unifying" laws of biology, on analogy with physical laws, such as the second law of thermodynamics. Indeed, he often compares his enterprise with physics and compares the statistical properties of genes in populations to the aggregate behavior of molecules in a gas (Fisher 1922). As M. J. S. Hodge (1992a) has argued, Fisher was strongly influenced by two nineteenth-century figures, Boltzmann and Darwin, whom he saw as ushering in a new, "indeterministic" scientific worldview—one that admitted of probabilistic explanations, or explanations that took the action of aggregative effects in the context of populations of organisms or physical systems to be explanatory. Fisher took Boltzmann's second law of thermodynamics to "transmute probability from a subjective concept derivable from human ignorance to one of the central concepts of physical reality" (Fisher 1932, 9). Fisher compares and contrasts his fundamental theorem of natural selection with the second law of thermodynamics:

> The fundamental theorem proved above bears some remarkable resemblance to the second law of thermodynamics. Both are properties of populations, or aggregates, true irrespective of the nature of the units which compose them; both are statistical laws; each requires the constant increase of a measurable quantity, in the one case the entropy of a physical system and in the other the fitness, measured by m, of a biological population. As in the physical world we can conceive of theoretical systems in which dissipative forces are wholly absent, and in which the entropy consequently remains constant, so we can conceive, though we need not expect to find, biological populations in which the genetic variance is absolutely zero, and in which fitness does not increase. (Fisher 1930, 37)

In other words, in his fundamental theorem, Fisher thought he had discovered a fundamental principle of biology, akin to the principle of entropy, though he also believed there were "profound differences" between the two. Biological systems are impermanent, whereas energy is never destroyed; fitness is qualitatively different for every organism, but entropy is the same across physical systems; fitness may be increased or decreased by changes in the environment; entropy changes are irreversible, while evolution is not.[3] And entropy leads to progressive disorganization, while evolution leads to "progressively higher organization" in the organic world.

This last comparison, between evolution as a force for progressive organization, and entropy leading to disorganization, was the core of what Hodge calls Fisher's "two-tendency" view of the universe. One tendency admitted of creative change, another of progressive loss of order. Fisher saw the second law of thermodynamics and the fundamental theorem as similar in that both are statistical laws that capture a fundamental dynamic between population-level properties—either of physical system or biological populations. Whereas entropy captures the dynamics between energy and time, the fundamental theorem captures natural selection's dependence on the chance succession of favorable mutations.

It is no accident that Fisher saw this parallel between physics and biology. He had postgraduate training at Cambridge with James Jeans in statistical thermodynamics and was particularly influenced in his thinking about evolution by innovations in physics, such as Maxwell's work on the properties of gases. As M. J. S. Hodge (1992a), J. R. G. Turner (1987), Morgan and Morrison (1999) and Depew and Weber (1995) have argued, Fisher transposed this mode of thinking, for example, about the physics of gases, from physics to evolutionary biology. Probabilistic models were, for Fisher, not an expression of ignorance, but a way of representing stochastic change in aggregative systems, such as populations of organisms or molecules in a gas (Fisher 1922).

Fisher's major work, *The Genetical Theory of Natural Selection* (1930), was a sustained defense of his interpretation of Darwin's view: namely, that selection acts gradually on "Mendelian" factors, or mutations of small effect. Fisher mentions chance eighty-one times in the *Genetical Theory*. The most common sense of chance to which he appealed was as proxy for probability. In the *Genetical Theory*, chance plays an important role in evolution in at least three senses. First, on the "particulate" or Mendelian theory of inheritance, chance enters into evolutionary explanation insofar as there is indiscriminate sampling via the random combination of genes. Second, Fisher (1922, 1930) argued that drift, or what he would call the "Hagedoorn effect," that is, "fortuitous fluctuations in genetic composition," played a role in evolution, though he tended to assume that effective population sizes were large, and so the rate of loss of alleles due to drift was low. The notion of effective population size is derived from the Wright-Fisher model: a simple model for the representation of change in populations over time, which assumes constant population size, nonoverlapping generations, and no mutation, recombination, selection, or population structure. Essentially, the model is a "null" model, representing change over time as entirely due to a random sampling process (with replacement) from one generation to the next. This model was taken to capture the

variety of ways in which populations are subject to "random" fluctuations in allele frequencies: for example, fluctuations in population size, extent of inbreeding, overlapping generations, and/or spatial dispersion. Wright (1931) and Fisher independently calculated the probability of fixation of one or another variant of a gene under such a simple sampling regimen.

Third, and finally, with respect to selection, Fisher emphasized that fitness is a probabilistic cause of change. Fisher remarks:

> We are now in a position to judge of the validity of the objection which has been made, that the principle of Natural Selection depends on a succession of favourable chances. The objection is more in the nature of an innuendo than of a criticism, for it depends for its force upon the ambiguity of the word chance, in its popular uses. The income derived from a Casino by its proprietor may, in one sense, be said to depend upon a succession of favourable chances, although the phrase contains a suggestion of improbability more appropriate to the hopes of the patrons of his establishment. . . . It is easy without any very profound logical analysis to perceive the difference between a succession of favourable deviations from the laws of chance, and on the other hand, the continuous and cumulative action of these laws. It is on the latter that the principle of Natural Selection relies. (Fisher 1930, 37)

Here Fisher is quite clear that natural selection is in many ways the exact opposite of "mere" chance, in the sense that it yields outcomes that are unequally probable. Just as casinos can profit from gambling (on average), so too, selection can act to change populations over time.

Perhaps the best way to understand Fisher's view on the role of chance in evolution is to consider his 1934 paper "Indeterminism and Natural Selection." Fisher there argues that current physics endorses an "indeterministic view of causation," by which he means both (1) that appeals to probabilistic causation have become far more common in science, for example, in statistical mechanics, and (2) that physicists endorse the "principle of indeterminism," or quantum indeterminacy. His central argument in this paper is that an indeterministic view of the natural world is a more "unified" and comprehensive basis for modern science: "Besides unifying the concepts of natural law held in diverse spheres of human experience, the view that prediction of future from past observation must always involve uncertainty, and, when stated correctly, must always be a statement of probabilities, has the scientific advantage of being a more general theory of natural causation, of which complete determinism

is a special case, possibly still correct for special types of prediction" (Fisher 1934, 104). That is, Fisher saw in physics a model for the lawful treatment of aggregative behavior in biology; probabilistic causes are, it seems, no less "real" than deterministic ones, provided we consider causal behavior of aggregative systems. Fisher holds that indeterministic behavior at the micro level could give rise to probabilistic behavior at the macro (see also M. J. S. Hodge 1992a). Fisher argues that "only in an indeterministic system has the notion of causation restored to it that creative element, that sense of bringing something to pass which otherwise would not have been, which is essential to its commonsense meaning" (Fisher 1934, 106–7). By "that creative element," Fisher appears to be referring to both to human agency and the capacity of natural selection to create genuinely novel adaptations; he is also replying to the work of authors like Bergson and Smuts, whose views of "creative" evolution required a special agency. Fisher contested that the creative elements of evolution did not require a jettisoning of mechanistic explanation, but of determinism. In a deterministic world, the human capacity for choice (and purposive behavior in animals, generally) is not real, but rather must be *illusory*. Yet, Fisher takes the purposive behavior of animals to be evident "not as an epiphenomenon, but as having a real part to play in the survival or death of the organisms that evince them" (1930, 108). In other words, since purposive behavior is a genuine cause of evolutionary change (organisms act and interact with one another and their environments, thus shaping their own genetic fate) and genuinely purposive behavior is inconsistent with determinism (on his view), indeterminism appears to be the only view consistent with evolutionary explanation. The argument is a sort of transcendental deduction of the necessity of indeterminism. M. J. S. Hodge (1992a) and J. R. G. Turner (1987) link Fisher's vision for a "creative" biology to his political (eugenic) and religious (Christian) commitments. Although these political and religious views do not directly influence his views about the role of chance in evolution, they certainly influenced his views about the significance of selection as a power for improving not only society, but also complexity and adaptation in the biological world.

Haldane

Haldane, like Fisher, was a "synthesis" thinker, though Haldane's biological interests ranged further. At one time or another in his life, he made major contributions to biochemistry, biochemical genetics, human genetics, statistics, theories of the origin of life, and evolutionary biology. Undoubtedly, his greatest contribution was his quantitative or statistical interpretation of evolution

by natural selection in light of Mendelian genetics as expressed in his series of papers entitled "A Mathematical Theory of Natural and Artificial Selection" (beginning with Haldane 1924a, 1924b, and continuing until 1934), in his book *The Causes of Evolution* (1932), and in his synthetic overview of genetics, *New Paths in Genetics* (1942). In those works, he sought to defend Darwin's theory of natural selection as the primary cause of adaptive evolution. Along the way, he gives some telling commentary on his views on fundamental physics, indeterminism, and implications for eugenics and human freedom.

In all these works, Haldane mentions chance very infrequently, only sixteen times in *The Causes of Evolution*, and the vast majority of these times, he is using the term *chance* as proxy for *probability*. The infrequency with which Haldane discusses chance suggests that he regards it as having a relatively less significant role in adaptive evolution than selection. In fact, Haldane is yet more explicit: "in a numerous species," the reduction of genetic variation as a result of drift would take "a long period even on an astronomical, let alone a geological time scale" (Haldane 1932, 117). For example, Haldane considers Elton's (1924) appeal to chance in explaining the evolution of the arctic fox in Kamchatka. Elton argued that on a fairly regular basis, modern arctic foxes suffer catastrophic population loss, or regular incidences of random extinction. As a consequence, effective population size for the arctic fox is very low. So the effect of drift should be large. In effect, Elton argues that random extinction is a significant cause of evolutionary changes in the fox. Haldane objects to this line of reasoning on the grounds that even with such drastic reduction in population size, the chance of loss of an allele is small, and ecological conditions could change dramatically throughout. In his view, such highly variable ecological conditions likely played a more significant role in the arctic fox's current state than drift. In sum, Haldane claims that "random extinction has probably played a very subordinate part in evolution" (Haldane 1932, 117).

One last point is worth mentioning. On the role of chance in mutation, Haldane makes the following (somewhat obscure) comment: "Muller has discovered how to control the rate of mutation, and it is clear that mutation is accidental rather than providential" (Haldane 1942, 20). Haldane here is making reference to the role of radiation in inducing mutation. With the publication of the paper "On the Nature of Gene Mutation and Gene Structure" by Timoféeff-Ressovsky, Zimmer, and Delbrück in 1935 (known as the Three-Man Paper; translation in Sloan and Fogel 2011), most geneticists, Haldane included, at this time would have known that irradiation increases the mutation rate, proportional to the applied dose, though exactly how this happened was relatively unknown. What Haldane means by "accidental" here, in contrast to

"providential," seems to trade on two senses of the term: first, that whether a given mutation occurs at one place or another on the chromosome is a matter of chance, and second, that mutations are by and large likely not to be advantageous (see Merlin, this volume, chap. 7, for a discussion of recent research on mutation). So, while this is far from explicit, Haldane seems to think the chance of an advantageous mutation's arising is more or less a product of indeterministic forces, or, at least not "providential" ones.

Wright

Sewall Wright is best known for his "shifting balance" theory of evolution, which he outlined in a series of papers between 1930 and 1932 (S. Wright 1930, 1931, 1932). Wright's arguments in these papers were hugely influential in both the early and the late synthesis. Particularly influential was his metaphor of the adaptive landscape, a multidimensional representation of fitness (in both individuals and populations) as a product of different combinations of genes. Wright's views about the relative importance of chance in evolution are best seen within the context of his shifting balance theory.

The shifting balance theory was Wright's answer to what he understood to be the "central question" of evolution. Wright noticed in his work on the evolution of coat color in mammals, and in his work at the USDA, that mass selection is effective but does not result in optimal traits. How then can genuinely novel gene combinations arise? Wright conducted experiments that suggested that inbreeding in general leads to a decline in fitness but can also lead to novel trait combinations. He became convinced of the advantages of combining selection with inbreeding within herds, followed by crossbreeding. The isolation of small subpopulations, followed by migration and thus shifting an entire population to new "adaptive peaks," was thus a way to answer the problem of how novel adaptive gene combinations might come about. Hodge nicely sums up Wright's central question (and answer) thus: "Under what statistical or populational conditions is this cumulative change most rapid, continual and irreversible, with or without environmental variation or change? Wright's answer is: When a large population is broken up into small local subpopulations with only a little interbreeding among those subpopulations, and when there is inbreeding, random drift and selection within those subpopulations, and when one or more subpopulations having individuals with selectively favored, superior gene combinations exports those individuals to other subpopulations and so contributes to transforming the whole population, the entire species" (M. J. S. Hodge 2011, 31).

As is clear from the above, chance plays multiple roles in Wright's shifting balance scenario, at various *levels* as well as *stages* of the evolutionary process. There is chance fixation of novel gene combinations in subpopulations, as well as the chance spread of these novel adaptive combinations through the entire population.

In the 1931 and 1932 papers, Wright mentions chance a total of thirty-two times; 63 percent of the time he refers to chance as probability and 37 percent of the time he refers to chance as randomness. He uses the word *chance* far and away more than anyone else, and he also uses it at higher rates. Although Wright speaks of chance playing a role in evolution in many different ways, he is most distinctive among all the early synthesis authors in seeing a role for drift in adaptive evolution.

Wright defines drift as the process by which "*merely by chance*, one or the other of the allelomorphs may be expected to increase its frequency in a given generation" (S. Wright 1931, 106, emphasis added). Similarly, in his 1932 paper, Wright defines drift as the process whereby "gene frequency in a given generation is in general a little different one way or the other from that in the preceding, *merely by chance*" (1932, 360, emphasis added). Thus, "merely by chance" refers to two distinct classes of causes: segregation/recombination, and reproductive stochasticity: "If the population is not indefinitely large, another factor must be taken into account: the effects of accidents of sampling among those that survive and become parents in each generation and among the germ cells of these" (ibid.). By "accidents of sampling," Wright is referring to the fact that in diploid organisms, one of two copies of an allele is randomly passed from each parent to an offspring as a result of recombination during meiosis. Alternatively, reproductive stochasticity concerns the possibility that, just by chance, some parents may have more offspring than others. As Wright puts it, "The conditions of random sampling of gametes will seldom be closely approached. The number of surviving offspring left by different parents may vary tremendously either through selection or *merely accidental causes*" (1931, 111, emphasis added). By "accidental causes," Wright appears to be referring to what we have called "contingent" events—for instance, living on the north rather than the south face of a mountain.

LATER SYNTHESIS

What we are calling the later synthesis was the period from roughly 1935 to 1950, during which there was an institutional reorganization of the field of biology, which involved the founding of the Society for the Study of Evo-

lution and the associated journal *Evolution*, as well as the organization of a variety of interdisciplinary conferences and book series, to promote evolution as a subject of study and to link existing disciplines—systematics, paleontology, and genetics. Though participants disagreed about which questions are most central to evolutionary biology, as well as which answers are most likely, all generally agreed on the consistency of the new genetics with a "Darwinian" view of evolution. What this Darwinian view amounted to was subject to various nuances, but all agreed on what Gould (2002) has called the "fundamental principles of Darwinian logic": that selection acts by and large on individual organisms, that selection leads to both genetic changes in populations (microevolution) and speciation (macroevolution), and that the very same causes of evolution in populations were responsible for the divergence of species and lineages. Moreover, all saw themselves as responding to various "opponents" to this "Darwinian" view, including anti-evolutionists, as well as "orthogenicists" and neo-Lamarckians. The core commitments of many of the latter synthesis authors were as follows:

- First, they saw their work as providing a "Darwinian" alternative to "directed" or "orthogenetic" views of evolution, according to which evolution has a predetermined direction.
- Second, they held that the origin (mutation) and sorting (recombination) of genes are in some sense chance or random processes.
- Third, all viewed natural selection as a probabilistic cause of adaptive change in populations.
- Fourth, all took the current distribution of species and adaptations as, in large part, a matter of contingency, both in terms of when and where mutations arise and are sorted in meiosis, and in terms of which environmental challenges are presented, that is, whether "contingent" events like storms, floods, and natural disasters were more or less in operation in the ecology and evolution of any lineage.

Dobzhansky

Genetics and the Origin of Species (1937) is a survey of biological work from genetics, population genetics, ecology, and natural history, as it bears on the fundamental problem of species' origins. In the first edition, Dobzhansky sees a significant role for chance in evolution, a role significantly diminished in the third (1951) edition. Dobzhansky speaks of chance operating in the spontaneous modification of chromosome structure, the distribution of chromosomes

during meiosis, and migration patterns and isolation of populations; and as featuring significantly in the fixation and loss of genes through random mating in small isolated populations.

One of Dobzhansky's central goals in 1937 was to defend the view that microevolution is sufficient for macroevolution. Dobzhansky argued that mutation is necessary, but no single mutation is *sufficient* for species level change. He argues:

> Species differ from each other usually by many genes; hence, a sudden origin of a species by mutation, in one thrust, would demand a simultaneous mutation of numerous genes. Assuming that two species differ in only 100 genes and taking the mutation rate of individual genes to be as high as 1:10,000, the probability of a sudden origin of a new species would be 1 to $10{,}000^{100}$. This is not unlike assuming that water in a kettle placed on a fire will freeze, an event which is, according to the new physics, not altogether impossible, but improbable indeed. (Dobzhansky 1937, 40)

Dobzhansky has a particular target in mind in this argument: the saltationist or "mutationist" view, defended by authors such as DeVries and Bateson. Interestingly enough, the argument itself appeals to improbability, and this was a rationale that many synthesis authors used to discredit defenders of "mutationist" or "orthogenic" theories of evolution. Though his book came out in 1940, Goldschmidt was roundly demonized by synthesis authors (particularly Mayr) for defending "saltational" evolution, or evolution by major "macromutations" (see, e.g., Goldschmidt 1940; Gould 1982).

While single mutations could not suffice to generate novel species, at the population level, Dobzhansky thought chance played a significant role. Dobzhansky notes that to some extent it is just a matter of luck whether a mutation becomes established in a population or whether it is lost: "A majority of mutations turning up in natural populations are lost within a few generations after their origin, and this irrespective of whether they are neutral, harmful, or useful to the organism. The numerous mutations which persist are the 'lucky' remainder which may be increased in frequency instead of lost" (Dobzhansky 1937, 131).

In other words, only a few offspring will inherit a newly mutated gene, and in species with a stable population size and a high rate of reproduction, it is a matter of luck whether those offspring will pass on the inherited mutation. Consequently, the vast majority of mutations, even those immediately benefi-

cial, are weeded out after a few generations. Only "lucky" mutations persist. While Dobzhansky does not use the term *genetic drift* in the first (1937) edition, he does follow Wright's lead, arguing that when a small population becomes isolated, simply by chance, some genes will become fixed and some will be lost: "Each of the colonies with very small breeding populations will soon become genetically uniform owing to the depletion of the store of the hereditary variability they once possessed. It is important to realize that in different colonies different genes will be lost and fixed, the loss or fixation being due, as we have seen, simply to chance" (Dobzhansky 1937, 134). In later editions, Dobzhansky refers to this process as "Drift" or the "Sewall Wright effect."

While Dobzhansky grants that mutations arise "by chance" and that the cause of mutation is unknown ("the name 'spontaneous' constitutes an admission of ignorance of the phenomenon to which it is applied" [1951, 38–39]), he does speculate on the causes of mutation (39). Dobzhansky cites a number of experiments in which mutation rates were increased with the application of radiation, iodine, potassium iodide, copper sulfate, ammonia, potassium permanganate, lead salts, and mustard gas (43). However, he is uncertain about the mechanism of mutation and hesitates to speculate regarding whether the ultimate explanation involves indeterministic causal processes, stating only that the outcomes are unpredictable: "X rays, ultraviolet rays, and the chemical mutagens mentioned above seem to be unspecific, in the sense that they increase the frequency of change (or destruction) of apparently all the genes of an organism. There is no way to predict just what genes will be found changed" (45). Dobzhansky seems to downplay the role of chance in later editions of *Genetics and the Origin of Species*. Beatty (1987) has argued, however, that Dobzhansky always viewed drift and selection as complementary and that his later emphasis on selection merely amounts to a shift in position on the relative *significance* of selection and drift. Beatty suggests that while Dobzhansky's empirical work on various laboratory species played an important role here, his primary motivators were his personal views in opposition to the "classical" versus the "balance" view of natural variation.[4] According to the classical view, often associated with eugenic ideology, most highly adapted populations are genetically uniform, suggesting that genetic variation in evolving (human) populations is ultimately detrimental. Dobzhansky strongly disagreed with this classical view and was firm in his belief that variation is absolutely necessary for the long-term survival and success of the human species. Thus, his ideological commitments in this context may have played an important role in his assumptions about the natural distribution of variation in most populations.

Mayr

Mayr's unique viewpoint was that of a systematist and a biogeographer. Mayr believed systematics and biogeography could yield insights into evolution that population genetics alone could not. In this sense one primary aim of *Systematics and the Origin of Species from the Viewpoint of a Zoologist* (1942) was to demonstrate the import of systematics and biogeography—or, perhaps better, the tradition of natural history—to the ongoing evolutionary synthesis. To achieve that aim, Mayr hoped to show how this perspective was essential to (1) explaining speciation, (2) providing additional evidence for gradualism, and (3) strengthening the case of the biological species concept.

Mayr argued that the "zoologist viewpoint" was better equipped to identify a *necessary condition* on speciation: nonbiological isolating mechanisms. Mayr argued that sympatric speciation was next to impossible and supported by little evidence, while allopatric speciation was much more common and supported by a rich body of evidence. For Mayr, if there were no barriers to random dispersal and mating, populations were unlikely to diverge. By necessity, then, portions of such populations must be reproductively isolated (either geographically or biologically) if new species are to arise. For Mayr, most cases of speciation will occur *after* a climatic (or geographic) event splits a single population.

Mayr uses the term *chance* merely eight times in the entire book, and in the majority of those cases, he refers to chance as proxy for *probability*. However, for Mayr, contingency does play a role in *geographic isolation* (most often the result of a climatic event). Both geographic and biological isolation (the result of selection on reproductive isolating mechanisms) are *necessary* to speciation, according to Mayr: "There is a fundamental difference between the two classes of isolating mechanisms, and they are largely complementary. Geographic isolation alone cannot lead to the formation of new species, unless it is accompanied by the development of biological isolating mechanisms which are able to function when the geographic isolation breaks down. On the other hand, biological isolating mechanisms cannot be perfect, in general, unless panmixia is prevented by at least temporary establishment of geographic barriers" (Mayr 1942, 226). If we attribute the production of geographic barriers to chance entirely, then chance plays an equally important role to speciation events as does natural selection of biological isolating mechanisms. Again, while he does not comment on the *relative* role of such chance events, there is room to argue that they played a fundamental role to Mayr's view of evolutionary speciation.

Simpson

In his *Tempo and Mode in Evolution* (1944), George Gaylord Simpson sets himself the primary task of synthesizing paleontology and genetics. To effect such a synthesis, he focuses on explaining the various causes of the "tempo and mode," or rates and patterns, of macroevolutionary change. Among those causes, Simpson places special emphasis on chance, which he refers to nineteen times in that single work. Of those mentions, 45 percent involved chance as probability, and 51 percent involved chance as randomness. In this section, we explicate what causal role Simpson attributed to chance to explain differences in tempo and mode.

By *tempo* Simpson means "rate of evolution," which he defines as rate of change of gene frequencies in a population relative to some absolute unit of time such as years or centuries. He favors defining rate of evolution as the "amount of morphological change relative to a standard," which might suggest a similar but not identical rate of genetic change (Simpson 1944, 3). The *standard* Simpson proposed for measuring rate of morphological change is taxonomic in nature. Specifically, Simpson proposed measuring rate of morphological change by dividing the number of successive genera by their total duration (17). For example, the line of successive genera starting with *Hyracotherium* and ending with *Equus* consists of eight genera and has a duration of approximately 45 million years. So the rate of morphological evolution, according to Simpson's standard, is 5.6 million years per genus, or .18 genera per million years. Using this standard of measure, Simpson describes the rates of morphological change for several genera. In this way, he establishes that there are differences in the tempo of evolution for different fossil groups or lines of successive genera.

Simpson identifies various *modes* of evolution: micro-, macro-, and megaevolution. The modes are individuated by taxonomic rank. So microevolution involves differentiation within a species but no "discontinuity"—that is, "branching" at the level of species or speciation. Macroevolution involves differentiation and discontinuity, including speciation as well as branching at the level of genera. Finally, megaevolution involves events at the micro- and macro- level as well as discontinuity at the level of higher taxonomic ranks such as families and orders (Simpson 1944, 97–98).

Simpson claims that population size plays "an essential role" as "a determinant both of rates and patterns of evolution" (Simpson 1944, 66). He shows that population size affects tempo, which in turn affects mode of evolution. Simpson reasons in the following way. First, he accepts Wright's argument

that large populations will exhibit high *variability* (i.e., *potential* for variation) but low *variation* and, consequently, will exhibit a slow tempo of evolutionary change. Selection will be either weak or strong in large populations. If it is strong, then even though the population is *variable*, selection will eliminate any *variation* that crops up. On the other hand, weak selection, Simpson argues, "tends to end in a static condition of fixed gene ratios" (67). In such cases, the mode will likely be microevolution.

Second, for Simpson, chance plays a role by increasing the tempo of evolution in intermediate-sized populations and, thus, produces discontinuities or branching events at the level of species or genera. This occurs for just the reasons Wright (1931) outlined. Intermediate-sized populations will exhibit variability similar to that of large populations. However, they will also be more susceptible to drift. So, although selection acts to eliminate variation, drift counters selection and maintains variation. Hence, intermediate population size is more likely to produce adaptive and discontinuous evolution (i.e., macroevolution).

Finally, Simpson considers small populations with little variability. Small populations face the same sort of difficulty as large populations: little variation available for evolutionary change. However, an adaptive mutation in a small population has a greater chance of fixation, or the "utilization of mutations in small populations is more efficient, that is, a single mutation has a much greater chance to survive or to become universal in the population and can do so much more rapidly" (Simpson 1944, 68). Simpson also appeals to Elton's (1924) *Random Extinction Model* and Wright's (1931) *Shifting Balance Theory*. Random extinction events like floods or catastrophes reduce population size drastically. Shifting Balance Theory involves variants going to fixation faster in small populations, so the tempo of evolution is significantly higher. Simpson argues that the number of successive, discontinuous genera produced by such rapid change may lead to higher taxonomic discontinuities at the level of family and order (i.e., megaevolution).

Stebbins

Stebbins's *Variation and Evolution in Plants* (1950), published in the Columbia Biological Series, is the last in a series of texts often identified as the "core" texts of the synthesis. The volume is also in many respects more comprehensive or synoptic than the earlier volumes, frequently drawing upon evidence and argument from the authors of both the early synthesis (Wright, Haldane, Fisher), and the latter synthesis. Stebbins's goal in this book is to summarize

advances in genetics, cytology, and the "statistical study of populations" and their import for the evolution of plants. The book is in some ways more comprehensive even than this, as Stebbins often pauses to compare and contrast evolution in plants and animals, discussing similarities in genetic "systems," modes of speciation, and the role(s) of population size and structure on evolutionary trends. Much like the *Origin*, the book opens with a discussion of variation and its causes and moves from a discussion of basic systematics and trends in variation among and between plants to their bases in environmental plasticity and genetic mutations. Second, Stebbins discusses the experimental and "historical" evidence for natural selection, pausing to consider causes of adaptive and apparently nonadaptive characteristics as well as correlation of characters. Third, he devotes a lengthy chapter to genetic systems as factors in evolution (where "genetic systems" are "internal" factors influencing the rate and nature of recombination and thus the rate and direction of evolution, which Stebbins argues is influenced largely by distinctive gene combinations) and moves on to the roles of isolation, hybridization, and various forms of polyploidy in speciation. The closing chapters in the book review long-term trends in the evolution of distinctive karyotypes and morphology, drawing upon both genetic and paleological data.

Stebbins takes a relatively equivocal view about the relative importance of selection and drift in evolution. He emphasizes that there is much that is as yet unknown about the intensity of selection, heritability, and the sizes of interbreeding populations in nature (Stebbins 1950, 39, 145). Even with this caveat, however, Stebbins indicates that "in cross-breeding plants natural populations are rarely maintained for a sufficient number of generations at a size small enough to enable many of their distinctive characteristics to be due to random fixation." In other words, Stebbins takes random fixation of genes in small isolated populations to be rare; for example, it may occur in cases where species are either confined to "highly specialized habitats" or reduced to small population sizes due to extreme environments or unusually drastic reductions in population size. Stebbins is clearly familiar with Wright's arguments, and he characterizes "random fixation of alleles" as instances of the "Sewall Wright effect," "undoubtedly the chief source of differences between populations, races, and species in nonadaptive characters" (144–45). However, he seems to think most populations of crossbreeding plants are relatively large, so that the chance of "random fixation" of genes is likely less significant than the effects of selection in such populations. Nonetheless, Stebbins does note that in the tropics, or island populations, there would be greater opportunity for nonadaptive differentiation due to random fixation.

Stebbins mentions chance twenty-nine times in the volume. The vast majority of instances are referring to chance as a proxy for "at random," as in "chance fixation" of alleles in isolated populations. Stebbins views such chance factors as potentially playing an early role in the differentiation of species and genera. Divergence, he argues, is most likely to result from special or unusual environmental agents that lead to isolation via "chance reassortment of different combinations of genetic factors" (1950, 508). Such appeals seem to echo Wright's shifting balance model, discussed above, transposed into the context of speciation and divergence. The second most common appeal is to probability, as in: "maximal chance for cross-pollination." The least common appeal is to "contingency." Most of his appeals of this sort involve a contrast with known or suspected causes (e.g., selection).

CONCLUSION

While it is clear from the above that the synthesis authors disagreed on many questions, they agreed upon the following points:

- Mutation is the ultimate source of variation, and mutations arise "by chance," where this is understood as "by and large assumed to be of deleterious effect" (or, not "directed" toward adaptation).
- Meiosis is a source of "random" variation (in sexual reproduction), the 50-50 chance of receiving alleles from either of two chromosomes.
- Isolation of small subpopulations is a source of "random" variation, in the sense that isolates may in many cases be treated as "random" samples from parent populations.
- Inbreeding is a source of chance gene combinations; that is, isolation of small (and thus genetically unique) subpopulations can be a source of evolutionary novelty.
- Drift can be represented as the sampling of alleles from a finite population, such that changes in population size are the main factors yielding an increase in "random fluctuations" in gene frequency.
- Drift and isolation may play a role in adaptive evolution and/or speciation, with new gene combinations arising in small isolated subpopulations.
- While it is unknown what the causes of mutation are at the submolecular level, the role of radiation in inducing mutation suggests, but does not prove, that indeterminism may play a fundamental role in evolutionary change.

- Contingent events play a significant role in macroevolutionary change—for example, due to catastrophic events such as geological and/or climatological changes, yielding extinctions, isolation of species/genera, and/or variable rates of macroevolutionary change.

In sum, synthesis authors shared a set of core commitments about the role(s) of chance in evolution. They agreed that chance plays an important explanatory role in evolution and that appeals to chance are not simply an acknowledgment of ignorance. Rather, appeals to chance (and its cognates) were to be interpreted as proxy for appeals to probability, random sampling, contingent events, or events in contrast to selection. Where they disagreed was about the *empirical* question of the relative *importance* of this or that chance factor in evolution. Some placed greater emphasis on drift than others, and, as we have argued, there was a pendulum shift from early to late synthesis; while Fisher and Haldane emphasized selection, Wright ushered in an emphasis on drift, which was later superseded by the "hardening" of views in favor of selection and downplaying the role of drift. To be clear, there was not a philosophical or conceptual transition in the synthesis, only a change in empirical views regarding whether and to what extent drift (as a matter of fact) was an important factor in evolutionary change. As we hope to have demonstrated, reading the works of authors of the modern synthesis is invaluable as a way of reflecting on core issues in the philosophy of biology. We have considered at least three interrelated questions that the texts of the modern synthesis can help illuminate:

The sense(s) in which evolution is a "probabilistic" theory.
The matter of whether (and in what sense) drift is a cause of evolutionary change.
The ways in which chance, contingency or accident is understood to play a causal role in evolutionary change, according to the synthesis authors.

Do these views provide us with insights into current debates among philosophers of biology, for example, about whether or not we ought to view natural selection (or drift) as causal? We begin with a caveat. It is our view that one should be extremely wary of reading philosophical claims back into historical texts, when these are not made explicit. Only rarely did these figures engage in explicit commentary on causation, metaphysics, indeterminism and determinism, or their relevance to biology. When they did, they were often quite

circumspect. Given how little they knew yet about mechanisms of inheritance in 1930, for instance, Haldane was very careful *not* to speculate as to how and why mutations arise, or whether their "random" character had anything to do with fundamental indeterminism. He was very careful to clarify that by the expression "mutations arise by chance," he meant "by chance *with respect to fitness*." In other words, mutations were not by and large fitness enhancing and did not arise in response to environmental conditions, as some Lamarckians claimed. When speaking of "random" events, synthesis authors were by and large very careful to specify what they meant, noting what empirical conditions would be of relevance to assessment of such claims. For example, Haldane explains: "By a population 'mating at random,' I do not mean one practicing sexual promiscuity, but one in which an individual is no more and no less likely to mate with a relative than an unrelated person, and no more and no less likely to mate with a person heterogeneous for the same recessive gene as himself than with a homozygous normal" (Haldane 1942, 149). That is, terms like *chance* or *random*, for these authors, by and large referred to very specific conditions, or facts about mating regimes, geographical isolation, or environmental contingencies, not "ignorance." So one should not read appeals to chance as asserting theories about the fundamental nature of the physical universe, such as commitments to fundamental indeterminism.

Nor should we attempt to read metaphysical presuppositions into mathematical models. It is certainly possible to agree upon how to represent evolutionary change in populations in mathematical terms and yet fundamentally disagree on questions ranging from whether natural selection or drift is a cause or not, to whether or not causation is acting at one or another temporal or spatial scale (as long-standing debates about levels and units of selection attest). That is, very little of great metaphysical import should be inferred from the endorsement of the empirical adequacy of a mathematical model. It is how the model is *interpreted* that tells us about the commitments of the authors of the model. That is, the use of statistical methods and models does not, in our view, discourage a reading of these authors as endorsing the thesis that heritable differences in organisms make a (probabilistic) causal difference to survival and reproductive success. Moreover, the very fact that these authors disagreed about the relative causal significance of selection versus drift for evolutionary changes in gene frequency suggests that they interpreted their theories as causal theories and that one can (and should) see drift and selection as distinct causes of evolutionary change. As Hodge (this volume, chap. 2) remarks: Fisher and Wright saw their "mathematical work as statistical analyses of causation, not as statistical replacements for causal analysis."

However, given their very different scientific and historical contexts, we ought not to expect that Haldane, Fisher, Wright, Dobzhansky, or Mayr would necessarily appreciate how current debates in philosophy are motivated or framed. For instance, one current debate in philosophy of biology concerns whether we ought to interpret evolutionary theory in "causal" or "statistical" terms. It seems to us that synthesis authors would see this as a false choice. Natural selection is meaningfully spoken of as a cause, in the sense that differential survival and reproductive success is (probabilistically) caused by differences in heritable traits; but, of course, the overall effects of this process can be observed only across generations and in populations. So it is represented at the population level in terms of population level variables, such as mutation rates, selection coefficients, and so on. Thus, in some sense, one represents the causes of changes over time as a "statistical" outcome, but Haldane's, Fisher's, and Wright's use of "statistical" models to represent population level variation, selection, and drift is hardly grounds to reject selection or drift as distinct causal processes. Clearly Fisher, Haldane, and Wright took them to be "causes" of evolution and did not (at least as far as we can discern) have metaphysical worries about whether causal processes are possible at the population level. Arguably, Fisher's creation of the analysis of variance (ANOVA) makes an implicit commitment to the very idea of partitioning causal variables at the population level. Wright, having worked for the USDA, would be very familiar with the use of population level variables and the role of artificial selection in intervening on everything from oil content in corn to milk yield. Haldane's aim in his popular book *The Causes of Evolution* is to demarcate and identify the major *causes* of evolution (and rule out other proposed causes). That is, we largely agree with Hodge's thesis (Hodge, this volume, chap. 2; among others, e.g., Okasha 2009; Millstein, Skipper, and Dietrich 2009; M. J. S. Hodge 1992a, 2011) that there was continuity between synthesis authors and Darwin regarding natural selection as a probabilistic cause of evolution.

We also agree that the contrast between drift and selection, for synthesis authors, was not between noncausal and causal processes but, as Hodge puts it, between "causally non-fortuitous and causally fortuitous" processes. Indeed, much of the work of the synthesis was to explain and describe the differences between such processes and how they made a difference in actual populations. They aimed to establish exactly which kinds of empirical information would be of relevance to deciding the causes of evolution in any case. In fact, arguably one of the central aims of synthesis authors was to distinguish merely hypothetical from actual causes of evolution, to provide em-

pirical evidence for the causes that they took to be central, and to provide a general mathematical framework for describing such causal processes, such that predictions and retroactive inferences about the relative role(s) of distinct causes could be precisely and empirically tested. We thus take it that they would also agree with Strevens (this volume, chap. 6) that there is certainly an objective distinction between drift and selection. Drift was not simply differential reproduction owing to causes we have so far failed to discern (pace A. Rosenberg 1994). The synthesis authors put a great deal of work into showing how to empirically distinguish the respective roles of drift and selection in actual populations. Establishing the role of drift requires, as Hodge puts it, "extra, decisive, detailed knowledge, not uninformed ignorance." As Strevens writes, "The great majority of serious evolutionary explanations citing drift are not . . . mere attributions of arbitrary deaths and wonky statistics to chance. They rather use mathematical models of evolutionary processes to make predictions about differential reproduction" (Strevens, this volume, chap. 6). That claim could well have been written by any synthesis author.

NOTES

1. While we do not follow their classification of senses of chance, we were certainly influenced in our classification by Millstein 2011; Gayon 2005; and Beatty 1984.

2. An initial draft included a section on Julian Huxley's *Evolution: The Modern Synthesis* (1942). While we think that this was without doubt a central book of the synthesis, for reasons of space, we could not include that section.

3. The claim that entropic changes are irreversible while evolution is not is misleading: entropic changes are indeed irreversible (which is why the second law is referred to as "Time's Arrow"), but evolution is also irreversible in its own sense. We may, for example, evolve large lizards again, but they will not be *T. rex* or *Brontosaurus*. Evolution can proceed from simple to complex and "degenerate" back to simple again (think of the branch of the annelid worms that became parasitic), but organisms are not really reversing the pathway or route by which they evolved. Thanks to Gar Allen for this comment.

4. We refer here to the "classical" versus "balance" views on whether populations are highly uniform at the genetic level, or variable. These views have been associated with Mueller and Dobzhansky, respectively.